Chapter 11

Reconstructing Lycopsids
Lost to the Deep Past

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Introduction: Plant Blindness and Its Influences
on Our View of Extinct Life Forms

Although plant communities define ecosystem structure in many modern landscapes in terms of biomass[1] and appearance, they receive less emphasis than animals in reconstructions of prehistoric landscapes. Plants associated temporally and palaeogeographically with prehistoric animals are often used as a background, serving to contextualize the focal animal subject, but they less often take on a central role in the ecosystems they help to comprise. Additionally, extinct plants have only rarely been depicted as focal subjects, independent of animals, or even their surrounding environment, and certainly not in meticulous detail – unlike, say, newly discovered dinosaurs. In many cases, long-extinct animals are reconstructed in great detail, while extinct plants are depicted in less detail, and vaguely resemble modern species[2] In summary: 'This form finds its most common expression as dinosaur art, characterized by a scrim of distant conifers, a pounded brown dirt foreground, and a centrepiece of fully realized dinosaurs in action poses. I call this form of dinosaur iconography "Monkey Puzzles and Parking Lots" for its regular reliance on stereotypical backgrounds that do not depict accurate vegetation'.[3] This is not an unexpected trend.

Plants are overlooked as organisms in their own right. The term 'plant blindness' was first used to describe a trend in the United States education system in which biology students perceive animals as having greater impor-

tance than plants, let alone other eukaryotes or prokaryotes.[4] This condition has been shaped, in part, by greater emphasis being placed by teachers on animals than plants. It has been argued further that plant blindness is just a facet of a much larger issue, which is that humans are conditioned to be everything-but-vertebrates-blind.[5] Given that 99 per cent of described terrestrial animal species are invertebrates,[6] overcoming plant blindness is a good start to creating a more empathetic connection to the diversity of life on Earth, which in turn could spur more inclusive efforts in conservation of biodiversity.[7] This literal and figurative anthropocentric view of plants as inanimate greenery is innate,[8] stemming from a snap-judgement decision-making process based on visibility bias in what is termed 'System 1'.[9] By contrast, those trained to study or appreciate plants beyond flashy flowers often engage in 'System 2',[10] a decision-making process that 'allocates attention to the effortful mental activities that command it, including complex computations'.[11] Plant blindness, moreover, has been found to be partially a physiological phenomenon, in that plants capture attention through the human visual system differently from animals.[12] In the case of 'seeing' plants, one has to grow accustomed to pausing to dedicate sufficient time and mental energy to observe their features, and therein to begin to appreciate their complexity, beauty and behavioural traits, as well as ultimately our full dependence on them as a foundation of many terrestrial food webs and living systems.[13]

Although extinct plants and the habitats they generated have and continue to be an integral part of palaeoartistic reconstructions, 'plant blindness', and overarching 'non-vertebrate blindness', have resulted in a vertebrate-centric visual culture. It is also natural to empathize more with organisms most similar to ourselves.[14] This is further compounded by the inherent difficulties of humans to comprehend 'deep time', a concept first described as a 'long Earth history' by Scottish geologist James Hutton,[15] and coined roughly two hundred years later by American author John McPhee.[16] Deep time (e.g. time spans of millions to billions of years), and the scale of geological and evolutionary processes over such long periods, are sublime to the human imagination. Accordingly, it is difficult to appreciate how profoundly organismal lineages, ecosystems and the appearance of landscapes have changed over such immense timespans. The art of depicting both the more familiar world and those alien worlds lost to the deep past is therefore crucial to contextualizing the history of life in modern ecosystems, and to learning how these systems themselves came to be.

While overcoming plant blindness in palaeoartistic reconstructions may seem a merely academic exercise, its consequences can profoundly impact our understanding of the history of life. The emphasis on which organisms are highlighted or emphasized in artistic depictions not only set a standard for which life forms should be considered important and interesting to the

general public, but also to children who someday will comprise the next generation of palaeobiologists. If children were to grow up getting to see meticulously detailed depictions focusing on extraordinary and beautiful plants, invertebrates and other biota as often as they do charismatic megafauna, it is likely they would have a greater curiosity to better understand life forms that are very different from themselves.

Charismatic Plants in the Fossil Record

The underrepresented realm of artistically reconstructed ancient plant worlds is itself shaped by numerous forms of favouritism. For instance, there are entire industries today that capitalize on our obsession with growing and displaying showy, colourful, animal-pollinated flowers in gardens over non-flowering plants. However, few of the most iconic 'primeval' plant lineages bear flowers. This is because many of these plant lineages diverged prior to the occurrence of the first discernible flowering plants in the fossil record (the Early Cretaceous Period; ~130 million years ago).[17]

Plants popularized in prehistoric imagery tend to fall into two major categories in public perception. First, 'plants of the dinosaur days' or 'plants that dinosaurs ate' – a measure of a plant's identity and value based on its utility to vertebrates.[18] These consist predominantly of seed-bearing plant groups such as ginkgoaleans, cycadophytes (cycads and bennettites) and conifers. Second, are the 'earliest' or 'most primitive' plants category, which are invariably also lumped into the category of 'dinosaur food'. Most often, horsetails and ferns are given this recognition by the public, although neither technically represents the earliest-diverging living vascular plant group.

Paradoxically, one of the most iconic, if not alien, groups of primeval plants is one the general public has seen in depictions but seldom heard of: lycopsids. This lineage of seed-free (spore-bearing) plants evolved a wide range of bizarre growth habits after diverging from all other vascular plants (those with lignified water- and nutrient-conducting tissues) over 415 million years ago. This division long precedes the divergence times for each of the remaining extant vascular plant lineages. Furthermore, lycopsids have survived all the major Phanerozoic mass extinctions since plants invaded land, and they persist to this day. They have always been evolutionary misfits, though are oddly ahead of their time compared to other vascular plants. Early in their evolutionary history, they became amongst the first vascular plant groups to evolve leaves, roots and a reproductive method that involves generating two different types of spores, giving rise to unisexual gametophytes (heterospory) that led to the development of structurally complex propagules in some lineages (e.g. lepidodendrids) that paralleled the evolution of seeds and pollen.[19] Moreover, lycopsids devel-

oped all these innovations independently of all other land plants, as the common ancestor to their group (lycophytes) and all other vascular plants (euphyllophytes) lacked roots, leaves and seeds.

In palaeoimagery, lycopsids have become a sort of botanical dinosaur, defying plant blindness, and somehow even eclipsing focal extinct vertebrates in reconstructions. In part, this is because most depicted extinct lycopsids occurred in the Silurian, the Devonian, and especially the Carboniferous Period (415–299 million years ago). In the late Silurian through to the Late Devonian, vertebrates were confined to aquatic realms, as they were all pre-tetrapod fishes. Therefore, terrestrial ecosystems were composed of microbial-, algal-, fungal-, lichen-, plant- and invertebrate-based food webs.[20] During the early stages of vascular plant diversification, lycopsids, along with their relatives and forerunners, were amongst the largest and most structurally complex multicellular organisms on land. From the Late Devonian through to the Carboniferous period – the Coal Age – arborescent (tree-forming) 'scale trees', or lepidodendrids, became iconic, towering statues, some species reaching over 50 metres (160 ft) tall, resembling gigantic telephone poles with open canopies of coral-like branches. These scale trees formed peculiarly sunlit, vast equatorial swamp forests,[21] whose remains comprise a considerable portion of the world's coal reserves. In Carboniferous swamp depictions, the giant lycopsids became a quintessential icon for the alien worlds dominated by giant arthropods before the age of dinosaurs. Given their historical and evolutionary significance, coupled with iconic visual status, how are these plants not more widely known by the general public?

One way to help to close gaps in the awareness of extinct plants may be for palaeoartists and/or scientists to make concerted efforts to visually reconstruct newly described fossilized plants or their structures in vivid detail and colour. Not only can compelling illustrations of the organism itself serve as a visual counterpart to technical descriptions, but colourful and photo-realistic illustrations capture the immediate attention of viewers (the snap-judgement visual bias of System 1),[22] and inspire more analytical viewing (System 2).[23] Such 'dinosaur-like' illustrations can, in theory, elevate plants to prehistoric animal-like recognition, and inspire renewed interest in extinct plants through public display.

Reconstruction: A Challenge at the Intersection of Scientific and Artistic Frontiers

Plants provide a conservative starting point for breathing life into ecosystems of the deep past. Although there are always exceptions to the rule,

plants have largely behaved and functioned in a remarkably predictable manner over the past 500 million years. They tend to be photosynthetic autotrophs – meaning, plants manufacture their own foods by converting solar energy, water and carbon dioxide into chemical energy in the form of sugars. Furthermore, all body plans of green algae and land plants are generated by five cellular developmental processes,[24] yielding four body plans, of which one is multicellular, comprising all land plants. With just a small number of developmental processes added, a seemingly endless array of body plan variations have evolved in land plants, all stemming from contrasts in timing, location and planes of cell division.[25] Colour, while variable in modern plants, also tends to be conservative, with renditions of green being most typical of photosynthetic tissues. Additionally, variations of yellows, oranges, reds, pinks, bronzes and purples are produced by a variety of UV-absorbing pigments, such as flavonoids, carotenoids and anthocyanins. Such 'sunscreens' are either concentrated in emerging foliage, or residually expressed when chlorophyll is drained from leaves during senescence, like deciduous trees in autumn. Blue to grey hues in foliage (glaucousness) can also result in plants under intense sun exposure. Under these circumstances, plants can exude thick, protective layers of reflective epicuticular waxes (farina) secreted from their outermost cells (epidermis) and membrane (cuticle), or through producing reflective hairs or glands on their outer surfaces. Furthermore, macro- and micronutrient availability as well as the degree of solar exposure can impact which shade of green an individual plant manifests, and also lead to predictable responses in leaf colouration, size, shape, orientation and damage. These traits and responses have evolved independently across numerous plant lineages, and – insofar as they are caused by structural changes of leaf surfaces – are preserved to some degree in the fossil record, making coloured reconstructions less of a guessing game for extinct species.

Despite their developmental and functional stability over geologic time, fossilized plants, especially wholly extinct lineages, can present challenges for reconstruction. Sporophytes (the largest, most frequently preserved life stage in vascular plants) are composed of three general organ classes: shoots, roots, and lateral appendages (e.g. leaves, reproductive structures). Many plants routinely produce and shed their outermost tissue layers and lateral appendages over time, such as leaves, branches and bark, as well as reproductive propagules such as spores, pollen and seeds. As context, it is not normal for animals such as vertebrates to jettison their body parts across the landscape. These organs, in turn, must land in an appropriate depositional environment where they have a chance of being preserved as fossils. Such environments enable preservation of organic materials through suppressing the metabolism of microbial decomposers, such as

cold temperatures, absence of oxygen, and extreme pH (highly basic or acidic environments). Plant parts can easily become damaged when travelling from the parent specimen to their site of preservation. Following burial, during the process of fossilization, what organic remains are still intact can be further altered by chemical and physical changes that occur as sediment becomes sedimentary rock over millions of years.

As a result of these processes, palaeobotanists are left with a fragmentary record requiring a skill set similar to a forensic investigator to piece together life forms of the past. They not only have the Herculean task of reconstructing organisms that no longer exist, but must often rely upon fragmentary, isolated organs to do so, and if possible, attempt to assemble extinct plants from these parts.[26] Furthermore, reconstructing extinct plants is heavily influenced by the 'pull of the recent' or 'pull of the present', in which views of modern plants shape how extinct species are reconstructed.[27] With plants that are long-extinct, unusual or fragmentary, using modern species as a blueprint for reconstruction can be either illuminating or limiting. One must carefully integrate detailed study of fossil morphology and anatomy with traits of nearest living equivalents to approach accurate reconstructions. Additionally, unlike vertebrates, it is also difficult to extrapolate the exact habit of an extinct plant beyond the organs that are preserved, due to the plasticity in plant body plan variations over the past 500 million years.

Whether the intact fossilized fragments of one organ match up with another, or belong to the same biological entity, requires detailed comparisons between new and revisited fossilized parts. Such comparisons depend upon observations of morphology (larger-scale, or macroscopic details), and, whenever possible, anatomy (cellular and microscopic details). When a fossilized plant is found to be attributed to a new species on the basis of morphology (morphospecies or morphotaxon), envisioning how the whole plant is three-dimensionally organized on the basis of two-dimensionally preserved compression fossils generates additional challenges to reconstruction.

Fortunately, the lycopsid branch of the tree of life has managed to survive multiple mass extinction events and has retained a strikingly conservative set of morphological traits.[28] Having undergone several major diversification events in the Late Paleozoic Era (~415–252 million years ago), only three lineages persist to this day: clubmosses and firmosses (Lycopodiaceae), spikemosses (Selaginellaceae), and quillworts (Isoëtaceae) (Illustration 11.1). Among the unifying characteristics of many extinct and extant members of this plant lineage are dichotomizing (bi-furcating) shoot and/or root systems, shoots bearing dense spirals of microphylls (small or simplified leaves containing only one vascular vein), and a single reniforme (kidney-shaped) sporangium [spore-bearing capsule] having a
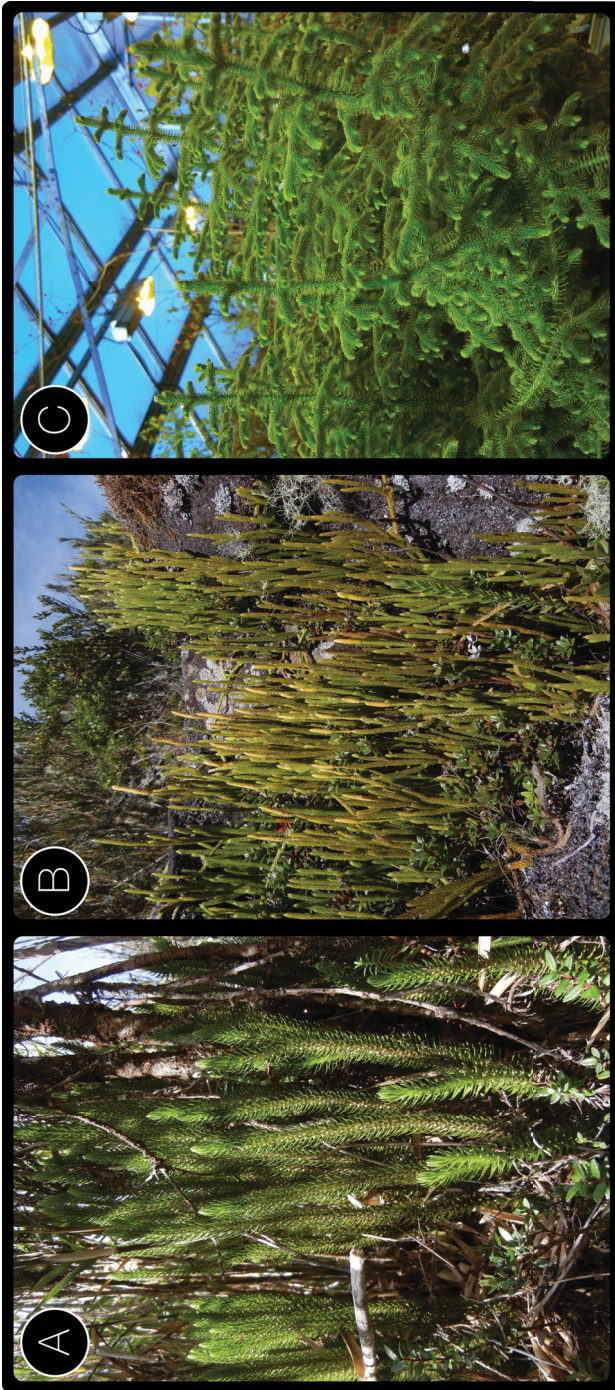
Illustration 11.1 Examples of living lycopsids (clubmosses and firmosses: Lycopodiaceae) from sunlit habitats similar to those used for *Leclercqia scolopendra* reconstruction. (A) *Phlegmariurus* (Herter) Holub sp., Cerro de la Muerte Massif National Park, Costa Rica; (B) *Lycopodium clavatum* var. *contiguum* (Klotzsch) Øllgaard, Cerro de la Muerte Massif National Park, Costa Rica; (C) *Palhinhaea* cf. *cernua* (Linnaeus) Vasconcellos & Franco (South African form), University of Washington Biology Greenhouse, Seattle, USA. Photos by author.

marginal clamshell-like opening on the adaxial (upper surface) per leaf. Despite maintaining conservative body plans through time, lycopsids can be challenging to portray faithfully. In particular, the multitudes of tightly inserted, spirally arranged needle- or awl-shaped leaves covering much of the shoot system can create substantial labour for artists, resulting in many reconstructions being generalized, resembling pipe cleaners or bottle brushes from a distance. In scientific descriptive illustrations, accurately placing the leaves is critical to demonstrating, as precisely as possible, how the plant may have appeared in life. Similar challenges can be presented when representing root morphology and habit in extinct lycopsids, as many modern species have roots densely clothed in fine wispy root hairs, and some extinct arborescent lineages had massive subterranean shoots (stigmaria) clothed in clouds of spirally arranged dichotomizing rootlets.[29] Through a case study reconstructing a shoot fragment of a Middle Devonian lycopsid, some challenges in extinct plant representation were overcome through an integrative study of morphological variation between extinct and extant lycopsids.

Reconstructing the Centipede Clubmoss

On Red Mountain, in Whatcom County of northern Washington State, an assemblage of black, two-dimensional, film-like compression fossils of early land plants were found on sheet-like slabs of early Middle Devonian (~375 million years)[30] sandstone.[31] Tiny, densely leaved lycopsid branch fragments were amongst the twig-like branches of numerous early relatives of ferns and seed plants. All these lycopsid fragments belonged to the genus, *Leclercqia* Banks, Bonamo and Grierson. However, amongst the fragments, there appeared to be two distinct morphotypes (morphologically different entities).

The leaves of *Leclercqia* are unusual for lycopsids. Rather than being simple and needle-like, like their closest living counterparts (clubmosses and firmosses, Lycopodiaceae; Illustration 11.1) those of this genus appear only simple at the base, but then divide into five to twelve segments away from the stem. In the type species, *L. complexa* Banks, Bonamo and Grierson, the leaf somewhat resembles the arched neck and long, curved bill of an ibis, adorned with pronghorn antlers in profile view – as is often their orientation of preservation in the fossil record. As such, the leaves attached to the stem look somewhat like miniature hunting trophies mounted to a wall. The result, in *L. complexa*, is a highly intricate, three-dimensionally pronged leaf with a central, downward-curved leaf segment and two pairs of lateral segments, splitting into prongs that project upwards and outwards.

At the time of collecting and describing the lycopsid fossils from Washington, only two species of *Leclercqia* had been described; *L. complexa* and *L. andrewsii* Gensel and Kasper. In *L. andrewsii*, the leaf base is flattened into one plane, curling upwards and dividing into five erect leaf divisions.[32] Because the leaves of all Washington specimens were oriented in the pronghorned-ibis-like, three-dimensional orientation, both morphotypes were most similar to *L. complexa*.[33]

Given some differences between fossils, it was not clear whether the more compacted branch fragments of *Leclercqia* with curved leaf bases, found in Washington, represented an oddly compressed *L. complexa*, a variety of that species, or an entirely new entity. In the scientific community, there are a range of considerations in determining which criteria are used to define a species of plant. Since fossils of old, extinct plants do not contain DNA, there is no way to compare their relation to each other or to modern species using cutting-edge molecular techniques. Morphology and anatomy therefore provide the only criteria upon which fossil plants can be assigned a species. Furthermore, some parts of plant bodies are assigned their own form genera names. For example, the branches, trunk, and root-bearing organs of the arborescent (tree-forming) lycopsids of the Carboniferous coal swamps all have different form genera names, even though they all come from the same tree specimen (and therefore a single species). These different form genera names exist because isolated organs of these plants were discovered at different times and only subsequently pieced together as belonging to the same organism. Additionally, it is well possible that, for instance, several distinct fossil species shared the same, morphologically indistinguishable type of root-bearing organs. As a result, the separate name for such root-bearing organs must be maintained alongside the species name for the whole plant.

Fortunately, there are no known form genera of *Leclercqia*, as these lycopsids are known exclusively from branch fragments. Traditionally, a new species of fossil plant could be assigned if it was qualitatively distinct enough in morphology from all other previously described species. For example, it might be argued that 'species X looks different from species Y and Z based on traits A, B and C. Therefore, species X can reasonably be described as a new entity, and it is hypothesized that it represents a separate species'. However, in the case of the two co-occurring *Leclercqia* morphotypes in the same sedimentary rocks of Washington State, there were clear similarities but also differences, and so a more detailed comparison was warranted. Rather than using a more conventional qualitative comparison, these *Leclercqia* morphotypes needed to be assessed by applying quantitative methods more often used in comparing variation between animals.

In order to more quantitatively determine whether the unknown morphotype represented a new species or variety, linear morphometric analyses were performed. This meant that a series of measurements were taken (in this case, the lengths, thicknesses and angles within a leaf) in leaves of as many intact specimens of the unknown morphotype as possible. These measurements were then compared to those taken on *L. complexa* species sampled from six continents. The same analyses were subsequently used to compare morphological variability between extant species and variants of modern clubmosses (Lycopodiaceae) grown in a greenhouse.[34]

It was found that the unknown *Leclercqia* morphotype from Washington was statistically significantly distinct from *L. complexa*.[35] Furthermore, these fossil lycopsids were as distinct from one another as the two modern clubmoss species compared are from each other. On the basis of these analyses, it was revealed that the unknown morphotype was very different from *L. complexa* in several key traits. The new morphotype was assigned to a new species: *Leclercqia scolopendra* Benca et Strömberg.[36] This species name means 'Centipede Clubmoss' based on the resemblance between its modular and tightly packed curved leaves with the legs of tropical centipedes in the genus *Scolopendra* (Scolopendridae).

Previous anatomical and morphological studies of *Leclercqia complexa* provided an excellent resource for reconstructing a structurally similar member of the genus in great detail by minimizing guesswork in interpreting fossils having less optimal preservation in Washington.[37] Typically, newly described fossilized plant species are reconstructed within the descriptive studies using detailed contour line drawings, rendered by hand. However, it became clear after several hand-drawn renditions based on the two-dimensional compression fossils of *L. scolopendra* that bringing life to this plant would present unique challenges. In short, something seemed to be lost in translation between the compression fossils and the initial illustrations, yielding reconstructions that were indistinguishable from *L. complexa*, which was inconsistent with the quantitative results.

By hand, it was difficult to anticipate exactly how the structurally intricate leaves of *L. scolopendra* would interplay amongst each other in three-dimensional space. Using the measurement data of a range of traits that quantified leaf shape, thickness, angle and orientation, it was possible to precisely render the leaves digitally in several different orientations using the vector software programme Adobe (San Jose, CA, USA) Illustrator CS6.[38]

Based on the spirally arranged scars left from detached leaves (resembling the inter-locking, ganoid scales of gar fishes) along the branch fragments of *L. scolopendra*, it was possible to render a stem fragment and know exactly where the leaves would be inserted (Illustration 11.2). After reconstructing anatomically precise leaves from multiple angles, it
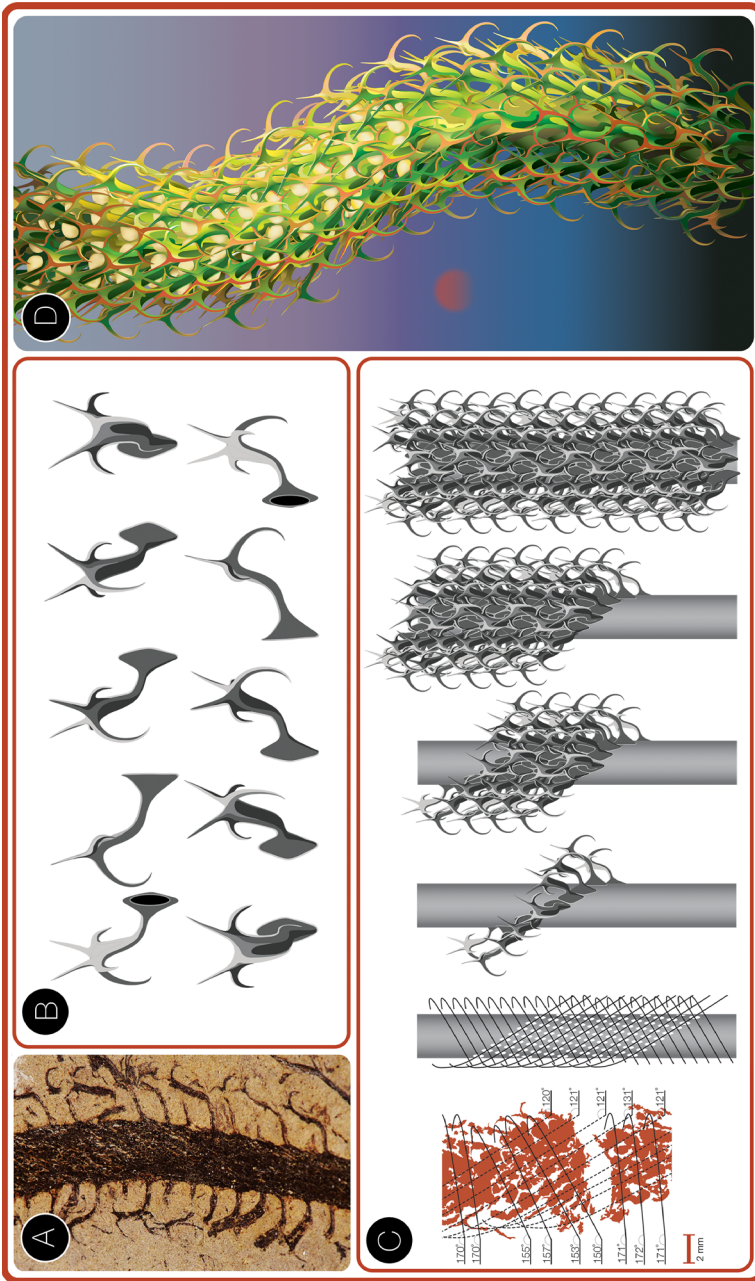
Illustration 11.2 Digital reconstruction process of *Leclercqia scolopendra* used to accompany the species description (Benca et al., 'Applying Morphometrics'). (A) Fossil fragment of *L. scolopendra*; (B) Digitally reconstructed leaves of *L. scolopendra* in different perspectives; (C) Process of reconstructing leaf arrangement (phyllotaxy) of *L. scolopendra* using fossilized leaf and sporangial insertion points; (D) Reconstruction of *L. scolopendra*. Illustrations rendered by author using the vector software program Adobe (San Jose, CA, USA, Illustrator CS6).

was then possible to insert the leaves and see how they interplayed three-dimensionally. The results were surprising. The hook-like leaf bases of *L. scolopendra* formed a shield-like barricade of erect fan-shaped leaf bases. However, even more surprisingly, the spine-like leaf segments formed an overlapping labyrinth of spines projecting in all directions (Illustration 11.2). Only by rendering the leaves as vectors digitally was it possible to see how they would precisely interlock and interact with each other along the branch.

This was an important point, because the extent to which the leaves overlapped would have been difficult to anticipate if only using one's imagination and sketching from hand. Any minor inaccuracy in the angle, attachment or proportionality of the leaves would yield an inaccurate, more sparsely arranged, structure. This was a barrier in artistic expression, because no human had ever seen a plant structurally arranged quite like *L. scolopendra*. After all, this plant has been extinct for over 375 million years and may have been easy to overlook as a fossil.

Reconstructing extinct life forms can be hampered by expectations that a fossil form would resemble something already known in the modern world. There are limitations to our imagination, and historic realities obscured by the fossil record can, do, and invariably will turn preconceived notions upside down with additional discoveries.

In the case of *L. scolopendra*, hand-drawn draft reconstructions looked more like modern clubmosses with cilate (hair-tipped) leaves. However, the digitally calibrated leaves and stem taken together made the final rendition look superficially more akin to a marine invertebrate than a plant – specifically a deep-sea glass sponge (a hexactinellid). In this particular case, using scientific data to inform the artmaking process resulted in a reconstruction that may have captured how a branch fragment of this extinct species would have appeared when alive 375 million years ago.

The final touch to artistically representing *L. scolopendra* came down to choices in colouration of the plant. As no fragments of early trees (e.g. *Archaeopteris*) were found in the Washington fossil beds, it seems likely that *L. scolopendra* was not growing near closed-canopy forests but instead occupied open, sunlit environments. Since many modern clubmosses continue to grow in open, sunlit environments, their colouration was used as a conservative guide. Moreover, after developing the first successful cultivation techniques for a wide range of terrestrial clubmosses,[39] it was possible to use clubmosses of several genera grown side-by-side under controlled greenhouse conditions as the references for developing the colour pallet of *L. scolopendra*. In extant Lycopodiaceae, most species occupying open habitats range in colouration between dark apple green to bright golden, yellow-green (Illustration 11.1). *L. scolopendra* was therefore depicted at

a midpoint of the spectra of modern Lycopodiaceae from sunlit habitats (Illustration 11.2D).

Sometimes the reconstruction of an organism can surface entirely new lines of scientific inquiry about an extinct organism. In the case of *L. scolopendra*, why the leaves formed such a complex three-dimensional cloud of spine-like segments was uncertain. Perhaps the shield-like leaf bases and projecting leaf segments were a form of protection to the developing sporangia from desiccation or herbivory (like the shielding leaves or bracts of developing cones).[40] However, such ideas of adaptive significance in structure are difficult to test or verify in the fossil record. Furthermore, no known stem fragment of *Leclercqia* or its closest relatives – members of the extinct lycopsid order Protolepidodendrales – are attached to rooting organs or rhizomes to date. It is therefore unclear whether stem fragments of *Leclercqia* come from a herbaceous, vining plant resembling modern clubmosses – as they have been traditionally envisioned[41] – or branch tips from canopies of telephone-pole-like trees.[42] In the case of *Leclercqia*, more complete fossils are needed to confidently undertake whole-plant reconstructions.

Conclusion

Accurate and conservative palaeobotanical reconstructions most often accompany scientific studies that can be difficult for the public to access. However, these works serve as indispensable guides for a growing number of palaeoartists undertaking more holistic ecosystem reconstructions that can, in turn, be presented to the public. The extinction rate of land plants is now up to five hundred times pre-Anthropocene background extinction rates.[43] It is therefore vital that the next generation of thinkers, scientists, activists and conservationists see plants for the incredible and charismatic organisms that they are.

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global ecosystem collapse under stratospheric ozone weakening, published in *Science Advances*.

Notes

1. Bar-On, Phillips and Milo, 'The Biomass Distribution on Earth'.
2. Manchester, Calvillo-Canadell and Cevallos-Ferriz, 'Assembling Extinct Plants'.
3. Johnson, 'Using Paleobotany to Make Better Reconstructions'.
4. Wandersee and Schussler, 'Preventing Plant Blindness'.
5. Knapp, 'Are Humans Really Blind to Plants?'
6. Wilson, *The Diversity of Life*; Larsen et al., 'Inordinate Fondness Multiplied and Redistributed'.
7. Berenguer, 'The Effect of Empathy'; Knapp, 'Are Humans Really Blind to Plants?'
8. Wandersee and Schussler, 'Toward a Theory of Plant Blindness'.
9. Kahneman, *Thinking, Fast and Slow*; Knapp, 'Are Humans Really Blind to Plants?'
10. Kahneman, *Thinking, Fast and Slow*.
11. Ibid.; Knapp, 'Are Humans Really Blind to Plants?'
12. Balas and Momsen, 'Attention "Blinks" Differently'.
13. Ibid.
14. Berenguer, 'The Effect of Empathy'.
15. Hutton, *Theory of the Earth*.
16. McPhee, *Basin and Range*.
17. Gomez et al., '*Montsechia*, an Ancient Aquatic Angiosperm'.
18. Knapp, 'Are Humans Really Blind to Plants?'
19. Phillips and DiMichele, 'Comparative Ecology and Life-History Biology'.
20. Shear and Selden, 'Rustling in the Undergrowth'.
21. Phillips and DiMichele, 'Comparative Ecology and Life-History Biology'.
22. Kahneman, *Thinking, Fast and Slow*.
23. Ibid.
24. Niklas, 'The Evolution of Plant Body Plans'.
25. Ibid.
26. Manchester, Calvillo-Canadell and Cevallos-Ferriz, 'Assembling Extinct Plants'.
27. Ibid.
28. Ambrose, 'The Morphology and Development of Lycophytes'.
29. Hetherington, Berry and Dolan, 'Networks of Highly Branched Stigmarian Rootlets'.
30. Brown, Gehrles and Valencia, 'Chilliwack Composite Terrane'.
31. Benca et al., 'Applying Morphometrics'.
32. Gensel and Kasper Jr., 'A New Species of the Devonian Lycopod Genus'.
33. Benca et al., 'Applying Morphometrics'.
34. Benca, 'Cultivation Techniques'.
35. Benca et al., 'Applying Morphometrics'.
36. Ibid.
37. Banks, Bonamo and Grierson, '*Leclercqia Complexa* Gen. Et Sp. Nov.'; Grierson and Bonamo, '*Leclercqia Complexa*: Earliest Ligulate Lycopod'; Bonamo, Banks and Grierson, '*Leclercqia*, *Haskinsia*, and the Role of Leaves'.
38. Benca et al., 'Applying Morphometrics'.

39. Benca, 'Cultivation Techniques'.
40. Benca et al., 'Applying Morphometrics'.
41. Liu et al., 'Reinvestigation of the Lycopsid *Minarodendron Cathaysiense*'.
42. Stein et al., 'Mid-Devonian *Archaeopteris*'.
43. De Vos et al., 'Estimating the Normal Background Rate of Species Extinction'; Nic Lughadha et al., 'Extinction Risk and Threats to Plants and Fungi'.

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